Article Addendum

The vital role of potassium in the osmotic mechanism of stomata aperture modulation and its link with potassium deficiency

Thomas T. Cochrane[1] and Thomas A. Cochrane[2,*]

[1]AGTECA S.A.; Mount Maunganui, Tauranga New Zealand; [2]Department of Civil and Natural Resources Engineering; University of Canterbury; Christchurch, New Zealand

Potassium deficiency symptoms of crops are well documented. However, the role of potassium in relation to the osmo-modulation of leaf stomata apertures was only discovered in the early 1970s. Our findings related to the differences between the osmotic properties of KCl and sucrose solutions provided an insight into that mechanism. In this report those findings are re-examined using a minor modification in the way their osmotic properties are calculated. The modification did not result in significant changes to the previous calculations. The properties of the KCl and sucrose solutions were subsequently compared with those of an extended series of inorganic and organic solutes. The calculations re-confirm that the osmotic properties of different solutes vary considerably. Research into the osmotic properties of solutes found in plant tissues may help elucidate other subtle plant physiological mechanisms. The findings highlight the vital role of potassium in plants. Its deficiency probably triggers a signal that results in the flow of potassium from the older leaves to support stomata modulation in the young leaves. This facilitates the survival of the plant, but leads to the necrosis of the older leaves and retarded growth.

Introduction

The symptoms of potassium deficiency in crops are well documented. Essentially older plant leaves necrose due to the evacuation of K^+ ions to the younger leaves.[1] Relatively recently in the early 1970s, it was recognized that potassium has a role in the opening of stomata aperture pores.[2-4] However the nature of its function remained speculative until our recent work comparing the different osmotic properties of KCl and sucrose.[5] In this article we review our findings and note the link to plant potassium deficiency. For comparison the osmotic properties of an extended series of organic and inorganic solutes has been recorded.

*Correspondence to: Thomas A. Cochrane; Department of Civil and Natural Resources Engineering; University of Canterbury; Private Bag 4800; Christchurch, New Zealand; Tel.: +64.3.364.2378; Fax: +64.3.364.2758; Email: tom.cochrane@canterbury.ac.nz

Calculation of the Osmotic Properties of Solutes

Our work on the role of potassium in the opening of stomata apertures[5] involved the use of the new equation[6,7] to calculate the several components of the osmotic potential of KCl as compared with sucrose in water solutions. The equation equates the relative energy of water molecules across a semi-permeable membrane interface separating pure water from a water-solute solution; it was originally formulated as:[8]

$$P_o = P_1 - P_x + P_y + P_h \qquad (1)$$

where: P_o = the osmotic or external pressure. The osmotic potential is the negative value of P_o. P_1 = the pressure exerted by pure water across the semi-permeable membrane interface separating it from a water solution. P_x = pressure exerted by the "free solution water", the water molecules of the solution in the theoretical absence of solutes. P_y = pressure lost by the free solution water to keep the solute molecules and, or ions, in solution. P_h = pressure lost by the free solution water to keep the water molecules very firmly held to the solute particles in the solution state. $\{P_1 - P_x\}$ is the difference between the pressure of the pure water and the "free solution water".

By using the new equation, the osmotic potential components P_1, P_x, P_y and P_h, were calculated separately for KCl and sucrose solutions by the sub-equations to Eq. (1) to compare the values of $\{P_1 - P_x\}$, P_y and P_h respectively for KCl and sucrose solutions at a temperature of 20°C.

In the new equation[6,7] P_h was calculated as:

$$P_h = P_1 N_h/N_w \qquad (2)$$

where N_h is the mean number of water molecules firmly held to the particles in solution and N_w is the number of water molecules per unit volume V in pure water.[5,6] Eq. (2) calculates P_h in terms of the pressure P_1 of the "pure" water. However, it was recently hypothesized that calculating this osmotic component in terms of the pressure P_x of the free solution water would provide an alternative test of the accuracy of the sub-equation. Consequently, for our current study P_h, was calculated as:

$$P_h = P_x N_h/N_f \qquad (3)$$

Table 1 **Osmotic pressure (O.P.) calculations of NaCl solutions at 20°C using the original sub-equation Eq. (2) in Eq. (1) compared with those of Marine and Fritz[10] and the calculations using the modified sub-equation Eq. (3) for calculating P_h**

NaCl. Concentration in kmol m^{-3}	Original with Eq. (2)	Osmotic pressure calculations (MPa)* Marine & Fritz[10]	Modified[1] with Eq. (3)	P_h calculations (MPa)* by Eq. (2)	by Eq. (3)[2]
0.103	0.448	0.469	0.450	1.866	1.872
0.207	0.914	0.931	0.914	3.764	3.762
0.311	1.389	1.406	1.357	5.662	5.651
0.418	1.878	1.892	1.880	7.590	7.594
0.523	2.374	2.374	2.370	9.519	9.501
0.631	2.885	2.879	2.882	11.479	11.460
0.757	3.485	3.476	3.487	13.750	13.746
0.866	4.021	4.001	4.019	15.741	15.723
0.995	4.657	4.631	4.658	18.074	18.061
1.106	5.218	5.182	5.218	20.100	20.072
1.218	5.796	5.745	5.789	22.149	22.101
1.331	6.382	6.325	6.375	24.202	24.146
1.445	6.988	6.932	6.976	26.286	26.209
1.599	7.807	7.772	7.804	29.055	28.995
1.715	8.447	8.415	8.441	31.170	31.091
1.832	9.108	9.082	9.094	33.416	33.205
1.930	9.664	9.646	9.652	35.090	34.975
2.029	10.240	10.028	10.225	36.894	36.762
2.330	12.052	12.081	12.031	42.369	42.190
2.534	13.341	13.400	13.319	46.071	45.864
2.741	14.711	14.789	14.685	49.835	49.587
3.056	16.936	17.032	16.903	55.559	55.244
3.270	18.561	18.644	18.576	59.447	59.080
3.486	20.313	20.363	20.274	63.367	62.945
3.928	24.383	24.277	24.317	71.424	70.829
4.153	26.758	26.857	26.651	75.499	74.826
4.382	29.485	29.500	29.402	79.667	78.879

The P_h values calculated by Eq. (2) are also compared with those by Eq. (3). *O. P. and P_h values calculated by substituting: t = 2.05 x 10^{-12} s, er$_w$ = 3.607 x 10^{-12} m, N_h = 4.5 and er$_p$ = 2.475 x 10^{-10} m, into the corresponding equations. Correlations: 1. R^2 = 1.00000 for the correlation between the original O. Pot. values calculated using the sub-equation Eq. (2) and those calculated using the modified sub-equation, Eq. (3). 2. R^2 = 0.99999 for the correlation between the P_h values calculated by Eq. (2) and Eq. (3).

where N_f is the number of "free" water molecules per unit volume of solution.[5,6] The osmotic potential components P_1, P_x, P_y and P_h, were re-calculated for KCl and sucrose water solutions for the -0.75 MPa, -1.5 MPa, -3.0 MPa and -4.5 MPa levels of osmotic potential. In addition the osmotic components of an extended series of inorganic and organic solutes, specifically: NH_4Cl, $CaCl_2$, $NaNO_3$, NaCl, D-fructose, D-glucose and D-mannitol, were calculated. With the exception of sucrose and NaCl, the calculations were carried out using the osmosity data[9] by substituting recorded NaCl values.[10] The concentration range for the sucrose calculations was the same as recorded by Slavik.[11]

Testing the Calculations

To examine differences in P_h values calculated by Eq. (3) compared with Eq. (2), osmotic pressure values for NaCl were calculated with Eq. (3) and compared with recorded values[10] as shown in

Table 1. The modification did not result in any significant changes; R^2 = 1.00000. Table 1 also records the calculation of the osmotic component P_h values using Eq. (2) compared with Eq. (3); they have a near perfect correction, R^2 = 0.99999.

Table 2 records the revised calculations of the osmotic potential components P_1, P_x, P_y and P_h for the KCl and sucrose solutions together with the extended range of solutes, at the solution osmotic potential levels of -0.75 MPa, -1.5 MPa, -3.0 MPa and -4.5 MPa. The precision of the osmotic potential calculations compared with recorded data are very high (Table 3).

Conclusions and Observations on a Probable Potassium Deficiency Signaling Mechanism

The calculations for NaCl recorded in Table 1 and those for KCl and sucrose and the other solutes recorded in Table 2 demonstrate that the modification to calculate P_h by Eq. (3) did not result in any

Table 2 **The components $\{P_1 - P_x\}$, P_y and P_h of the osmotic potential (O. Pot.) of KCl solutions compared with sucrose solutions and an extended series of inorganic and organic solutes at the -0.75 MPa, -1.5 MPa, -3.0 MPa and -4.5 MPa osmotic potential levels**

Solution O. Pot.	-0.75 MPa			-1.5 MPa			-3.0 MPa			-4.5 MPa		
O. Pot. components:	$\{P_1 - P_x\}$	P_y	P_h	$\{P_1 - P_x\}$	P_y	P_h	$\{P_1 - P_x\}$	P_y	P_h	$\{P_1 - P_x\}$	P_y	P_h
KCl: M conc.	←	0.171	→	←	0.336	→	←	0.667	→	←	0.990	→
O. Pot. (-MPa)	0.363	0.079	0.308	0.721	0.168	0.611	1.431	0.357	1.211	2.137	0.557	1.806
% of solution O. Pot.	48.4	10.5	41.1	48.1	11.2	40.7	47.7	12.0	40.4	47.5	12.4	40.1
Sucrose: M conc.	←	0.267	→	←	0.514	→	←	0.921	→	←	1.215	→
O. Pot. (-MPa)	0.637	0.113	0.0	1.226	0.274	0.0	2.203	0.797	0.0	2.912	1.588	0.0
% of solution O. Pot.	84.9	15.1	0.0	81.7	18.3	0.0	73.4	26.6	0.0	64.7	35.3	0.0
Extended Series[*]												
NH_4Cl: M conc.	←	0.170	→	←	0.334	→	←	0.653	→	←	0.960	→
O. Pot. (-MPa)	0.365	0.096	0.291	0.715	0.212	0.572	1.402	0.477	1.122	2.063	0.787	1.650
% of solution O. Pot	48.4	12.8	38.8	47.7	14.1	38.2	46.7	15.9	37.4	45.9	17.5	36.6
$CaCl_2$: M conc.	←	0.119	→	←	0.234	→	←	0.445	→	←	0.638	→
O. Pot. (-MPa)	0.322	0.115	0.313	0.631	0.256	0.614	1.204	0.629	1.167	1.734	1.092	1.674
% of solution O. Pot.	42.9	15.4	41.7	42.1	17.0	40.9	40.1	21.0	37.9	38.5	24.3	37.2
$NaNO_3$: M conc.	←	0.086	→	←	0.146	→	←	0.262	→	←	0.45	→
O. Pot. (-MPa)	0.362	0.073	0.315	0.728	0.146	0.626	1.459	0.291	1.241	1.954	0.436	1.853
% of solution O. Pot.	48.2	9.8	42.0	48.6	9.7	41.7	48.8	9.7	41.5	49.1	9.7	41.2
NaCl: M conc.	←	0.170	→	←	0.336	→	←	0.656	→	←	0.962	→
O. Pot. (-MPa)	0.344	0.097	0.309	0.682	0.206	0.611	1.334	0.473	1.193	1.956	0.800	1.748
% of solution O. Pot.	45.8	13.0	41.2	45.5	13.8	40.7	44.4	15.8	39.8	43.4	17.8	38.8
D-fructose: M conc.	←	0.297	→	←	0.571	→	←	1.057	→	←	1.455	→
O. Pot. (-MPa)	0.505	0.110	0.135	0.974	0.266	0.260	1.804	0.716	0.480	2.492	1.336	0.662
% of solution O. Pot.	67.3	14.7	18.0	65.0	17.7	17.3	60.1	23.9	16.0	55.5	29.8	14.7
D-glucose: M conc.	←	0.290	→	←	0.561	→	←	1.042	→	←	1.443	→
O. Pot. (-MPa)	0.511	0.096	0.143	0.985	0.240	0.275	1.834	0.655	0.511	2.543	1.250	0.707
% of solution O. Pot.	68.1	12.8	19.1	65.7	16.0	18.3	61.2	21.8	17.0	56.5	27.8	15.7
D-mannitol: M conc.	←	0.296	→	←	0.565	→	oor[†]					
O. Pot.(-MPa)	0.518	0.112	0.120	0.990	0.282	0.228	oor[†]					
% of solution O. Pot.	69.1	14.9	16.0	66.0	18.8	15.2	oor[†]					

The concentrations in kmol m3 of the solution solutes are shown at the several levels together with the percentages of the solution osmotic potentials (% of solution O. Pot.). The temperature of the solutions was 20°C. The P_h values were calculated using the modified equation Eq. (3). [*]Extended series of inorganic and organic solutes for comparative purposes. [†]oor = "out of the range" of the data recorded in Weast.[9]

Table 3 **Precision of the calculations of osmotic potential (O. Pot.) of the solutes recorded in Table 2**

Solute	Concentration range (kmol m^{-3})	O. Pot.* over conc. range (-MPa)	O. Pot. calculation factors		R^2 "O. Pot. v/s osmosity"[†]	No. of calculations
			N_h	er_p (m)		
KCl	0.135–1.890	0.593–8.699	4.5	1.4×10^{-10} m	0.9997	18
Sucrose	0.044–1.456	0.175–6.415	0	4.71×10^{-10}	0.9982	19
NH_4Cl	0.093–2.165	0.409–13.262	4.25	2.48×10^{-10}	0.9998	23
$CaCl_2$	0.045–0.617	0.275–20.316	4.33	3.075×10^{-10}	0.9965	27
$NaNO_3$	0.059–2.165	0.225–16.73	4.5	1.0×10^{-11}	1.0000	17
NaCl	0.103–4.382	0.448–29.485	4.5	2.475×10^{-10}	0.9999	27
D-fructose	0.028–1.738	0.064–5.6	2.6	4.27×10^{-10}	0.9998	34
D-glucose	0.056–1.873	0.138–6.66	2.66	4.27×10^{-10}	0.9993	18
D-mannitol	0.055–0.857	0.133–2.437	2	4.34×10^{-10}	1.0000	15

[*]O. Pot. = osmotic potential, calculated using Eq. (3) substituted in Eq. (1); the constant factors used in the equations for all the osmotic potential calculations were: t = 2.05×10^{-12} s and er_w = 3.607×10^{-12} m. [†]For the calculation of R^2, "O. Pot. v/s osmosity", with the exception of NaCl and sucrose, the values for the osmotic potentials of NaCl solutions as calculated by Marine and Fritz[10] were substituted for the equivalent osmosity values recorded by Weast.[9] The NaCl values were compared with the values calculated by Marine and Fritz and those of sucrose with the values estimated by Slavik.[11]

significant changes. This is because the intrinsic energy of the free solution water molecules would not be expected to vary from that of pure water. The tests re-confirmed the accuracy of the new equation which may use either Eq. (2) or Eq. (3) to calculate P_h.

The calculations in Table 2 re-confirm that at the same osmotic potentials of the solutions, the proportions of the components that contribute to their osmotic potentials are quite different.[7] They also re-confirm our findings to explain how the osmotic properties of KCl solutions versus sucrose, modulates the stomata aperture size during its diurnal cycle.[5] As we noted, the modulation mechanism minimizes the use of energy. It may also be observed that as sucrose is produced by photosynthesis in the leaves, taking advantage of that sucrose would add to the overall energy efficiency of the mechanism.

The study has re-confirmed the subtle role of potassium in the modulation of plant stomata apertures; by inference, the latter would be linked to potassium deficiency in plants. If potassium is deficient for a plant, it probably activates a signaling mechanism which leads to the translocation of mobile K^+ ions from old to new leaves to support stomata aperture osmo-modulation in the latter. This causes the breakdown of stomata in the old leaves and subsequent necrosis with the consequent loss of considerable leaf surfaces for the transpiration, gas exchange and photosynthesis processes for healthy plant growth; however it facilitates the plants survival. The vital role of potassium in the osmo-regulation of stomata apertures and the link with potassium deficiency in plants would warrant further investigations.

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